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Diverse patterns of larval coral reef fish vertical distribution and consequences for dispersal and connectivity

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Author Contributions

C. M. H. and J. K. L. conceived of the study. D. E. R., S. S., R. K. C., and J. K. L. carried out the field sampling. C. M. H., C. B. P., A. C. V., J. B. K., J. K. L. designed data analyses and model simulations. C. B. P. and A. C. V. developed modeling algorithm for the study. C. M. H. analyzed data and ran simulations, with computing support from B. T. J. C. M. H. wrote the manuscript. All authors edited the manuscript.

Open Research Statement: The empirical data used for this study and the release locations for the simulations are provided during review at <https://figshare.com/s/2439e43dbc614493b26f> and will be archived in Figshare upon publication. The newest operational version of the Connectivity Modeling System is available at <https://github.com/beatrixparis/connectivity-modeling-system>. The exact version of the CMS software used in this study is provided at <https://figshare.com/s/2439e43dbc614493b26f> for review and will be archived in Figshare upon publication. The GoM hydrodynamic model output is available at <https://www.hycom.org/data/goml0pt04/expt-20pt1>. The data obtained in 2013 for HyCOM global experiment number 60.5, 90.2, and 90.3 are no longer publicly available. Researchers should contact forum@hycom.org to request access to the specific experiment number that was used for this manuscript. Data from the same spatial and temporal coverage of this study can be obtained currently from HyCOM by using the query details

included in the files nest_1.nml (for global HyCOM) and nest_2.nml (for GoM), provided on Figshare.

Abstract

Many populations rely on dispersal as a critical life history event, from seed dispersal in plants to migration behaviors in birds, insects, and fishes. Species traits alter dispersal propensity and distance, and this in turn influences fitness. Vertical distribution behaviors, as have been observed in many taxa of fish larvae, are assumed to influence planktonic transport. Particular attention has been paid to the potential adaptive benefit of increased retention near the parental population due to ontogenetic vertical migration (OVM), in which larvae move deeper with age. By combining a large observational data set with individual-based modeling, we investigated the prevalence of OVM compared to other behaviors, and the effects of different vertical behaviors on dispersal and connectivity. We analyzed two years of monthly field observations of larval vertical distribution behaviors for 23 taxa of coral reef fish, with resolution across larval ontogeny. We found a diversity of behaviors both within and among coral reef fish families, with three prevalent patterns: surface-dwelling, ontogenetic vertical migration (OVM), and wide vertical spread. Using generalized versions of these three behaviors, we modeled larval dispersal throughout the Caribbean Sea over 5 years, for two pelagic larval durations (PLDs) that are typical of coral reef fishes. Models of surface-dwelling behavior generally led to longer-distance dispersal, lower local retention, and higher population connectivity than the uniformly-distributed and OVM behaviors. These latter two behaviors with deeper distributions during all or part of the larval stage had similar outcomes for dispersal, connectivity, and local retention. Similar impacts of behavior on dispersal, connectivity, and retention were observed under both short and long PLD. We also found that the effects of vertical behavior on larval dispersal were stronger than the effects of seasonal or interannual variation in currents. Our

results suggest that there are other advantages beyond higher local retention that contribute to the selection of a complex behavior such as OVM—these may include predator avoidance, temperature-driven metabolic changes, and the ability to overcome currents with directional swimming.

Keywords: connectivity, coral reef fishes, individual based modeling, larval dispersal, larval traits, local retention, ontogenetic vertical migration

Introduction

Dispersal is a fundamental life history process, influencing population demography, invasion dynamics, local adaptation, and gene flow (Kokko and López-Sepulcre 2006). In the terrestrial environment, many animals disperse via active movements (Nathan et al. 2008, Stevens et al. 2014), and many plants exhibit traits that increase their seed dispersal (e.g., fruits for animal-vectored dispersal, seed morphology that promotes wind dispersal; Tamme et al. 2014). Conversely, in aquatic environments, the fluid medium facilitates transport, and organisms are likely to exhibit traits that limit their dispersal (Burgess et al. 2016). Still, a pelagic larval phase is prevalent in marine taxa, and the processes governing the transport of pelagic larvae and their subsequent arrival at suitable settlement habitat are not fully resolved (Pineda et al. 2007, Cowen and Sponaugle 2009). The connectivity of suitable habitat patches has implications for population persistence, including the resilience and replenishment of disturbed communities and their dynamics (Hanski 1998, Hastings and Botsford 2006, Aiken and Navarrete 2011, Thrush et al. 2013). Shallow-water coral reefs are a canonical example of patchy habitat. The study of population connectivity is critical for conservation of coral reefs and management of the associated fish populations (Botsford et al. 2001, Burgess et al. 2014).

Direct measurements of dispersal in the marine environment are not only difficult and rare (Kinlan and Gaines 2003), but do not provide a mechanistic understanding of the processes involved. Therefore, individual-based modeling is a valuable tool for investigating connectivity of marine populations (Werner et al. 2007). In the past 15 years, major advances in computing power have enabled the development of high-resolution models of ocean currents and their use in increasingly complex biological-physical models. These models can now incorporate more biologically-realistic larval behavioral traits that may change during development, notably,

vertical distribution, swimming ability, and orientation (Edwards et al. 2008, Staaterman et al. 2012, Sundelöf and Jonsson 2012, Paris et al. 2013b, Rypina et al. 2014, Vaz et al. 2016).

Despite the increasing model capabilities over the past 15+ years, most recent Lagrangian modeling studies of larval dispersal still treat larvae as passive tracers (Swearer et al. 2019).

Of course, even small organisms are not entirely passive in moving fluids, since a variety of traits can modulate their dispersal (Nathan et al. 2008). In the highly diverse coral reef fishes, dispersal can be influenced by developmental rate, swimming abilities, and depth preferences (Paris et al. 2007, Staaterman et al. 2012, Sundelöf and Jonsson 2012, Rypina et al. 2014). For example, innate or environmentally driven differences in developmental rates affect the pelagic larval duration (PLD), or the length of time in the water column, which sets an upper limit for the scope of larval dispersal (Sponaugle et al. 2002). The few studies on the depth distributions of larval coral reef fish during their pelagic phase highlight taxon-specific behaviors (Leis 1991, Cha et al. 1994, Huebert et al. 2010, Irisson et al. 2010), and, due to vertical differences in ocean current velocity, such differences should influence dispersal (Irisson et al. 2010, Huebert et al. 2011). Of particular interest are patterns in vertical distributions related to larval age or ontogeny. Ontogenetic vertical migration (OVM) is characterized by a downward trend in depth distribution with larval age (Paris and Cowen 2004, Irisson et al. 2010) and, amongst modeling studies that include depth behavior, OVM behavior is commonly used (Paris et al. 2007, Butler et al. 2011, Staaterman et al. 2012, Yannicelli et al. 2012, Kough and Paris 2015, Vaz et al. 2016, Truelove et al. 2017). Additionally, OVM has been proposed as an adaptive mechanism for constraining larval dispersal with Ekman transport, particularly in locations where deeper flow can deliver older larvae back to shore (Paris and Cowen 2004, Drake et al. 2013). However, it is

not clear how widespread this behavior is across taxa or how regional variability in flow and bathymetry modulate its effect on retention and connectivity.

Among the studies that do incorporate larval fish traits and behaviors into dispersal modeling, they have, so far, been parameterized for a single species at a specific location (e.g., (Vaz et al. 2016) or compared drastically different species (e.g., Kough and Paris 2015). Here we instead take a general approach to understanding how vertical behaviors influence the dispersal of otherwise similar larval coral reef fishes, with broad spatial and temporal replication.

We had two overarching goals, each with specific research questions. First, we used empirical observations on the vertical distribution behaviors of Caribbean coral reef fish larvae to answer: How variable are taxon-specific vertical distribution behaviors, and how common and widespread is OVM? Our second goal concerns the consequences of differing vertical distributions on dispersal and connectivity, including the presumed adaptive benefit of OVM behavior to constrain dispersal. Specifically, we answer: How do dispersal, connectivity, and local retention for larvae exhibiting OVM behavior compare with a surface-oriented pattern and a uniform distribution? And, can the latter behavior generate similar patterns as OVM?

We addressed the first goal by analyzing the vertical behaviors of larvae of 23 taxa of coral reef fishes, from the most comprehensive observational dataset on larval vertical behaviors currently available. We also used these field observations to generate an empirically-derived OVM behavior. To address the second goal, we simulated larval trajectories exhibiting OVM, surface, and uniform vertical distribution behaviors, under two PLDs, to examine dispersal and connectivity across the wider Caribbean reef system over five years of daily releases. Our study shows that vertical behaviors are diverse, that surface-oriented taxa disperse farther and exhibit wider connectivity, that the uniform distribution behavior yields dispersal and connectivity

comparable to that of OVM, and that vertical behaviors interact with habitat availability and hydrography to generate complex local-scale patterns.

Materials and Methods

Field Sampling—Between January 2003 and December 2004, a transect of 17 stations across the Straits of Florida was sampled monthly for fish larvae (details in Llopiz and Cowen 2008).

Larvae were collected with a 4-m² multiple opening-closing net and environmental sensing system (MOCNESS; Wiebe et al. 1976, Guigand et al. 2005) and a 1 x 2 m neuston net, both with 1-mm mesh. The MOCNESS nets each sampled approximately 25 m of water depth, with four target depth bins: 0-25 m, 25-50 m, 50-75 m, and 75-100 m. The neuston net sampled the upper 0.5 m of the water column. Nets were outfitted with flowmeters to estimate the volume of water sampled during each tow. Plankton samples were preserved in 95% ethanol and later transferred to 70% ethanol. In the lab, larvae were sorted and identified to the family, subfamily, tribe, or genus level. Of the 55,603 coral reef fish larvae that were identified, over 9000 larvae were measured to provide the size-class-specific vertical distribution results presented here.

Measured larvae came from every other monthly cruise (starting with February, with January and March also included for 2003) and every other station across the Straits of Florida (for a total of 8 stations). Within each station–depth bin combination, all larvae for each taxon were measured for standard length up to a maximum of 30 randomly selected individuals.

Data Analysis—In order to identify common vertical behaviors, we calculated proportions at depth by size class (as a proxy for age) for 23 coral reef fish taxa: 14 families, 2 subfamilies, 1 tribe, and 6 genera. We used data from stations where the full targeted depth range of 0 to 100 m could be sampled (i.e. bottom depth >100 m, occurring at 16 of the 17 stations). For each study

taxon, we binned the measured larvae into three size classes; to ensure sufficient numbers of larvae in the largest size class, we set the length bins to 25% (size class 1), 25% (size class 2), and 50% (size class 3) of the observed size range. Further details on length data are available in Appendix S1 and Appendix S1: Table S1.

Larvae were also separated into depth bins. The MOCNESS net samples were classed according to their target depth range (0-25, 25-50, 50-75, and 75-100 m). Larval abundance (ind. m⁻²) for each net was calculated as: $a_i = \frac{n_i}{v_i} * h_i$, where n_i is the number of individuals collected in the net, v_i is the total volume filtered by that net, and h_i is the range of depth sampled (Irisson et al. 2010). The range of depth sampled was set to 0.5 m for the neuston net, but for the MOCNESS nets, the range was determined from the actual minimum and maximum depths recorded. The 0-25 m MOCNESS net did not sample neustonic waters well, so we summed the abundance (ind. m⁻²) for the neuston net samples and the 0-25 m MOCNESS depth bin. For each taxon, we produced proportions at depth for each size class. The proportion in a given depth bin is the sum of all sample abundances in that depth bin, divided by the sum of all sample abundances across the four depth bins.

Model simulations—We used the Connectivity Modeling System (CMS; Paris et al. 2013), an open-source individual-based biological-physical model, together with a 3D field of horizontal ocean currents. The CMS software enables multi-scale offline particle-tracking simulations in nested hydrodynamic models. We used horizontal currents from the global Hybrid Coordinate Ocean Model (HyCOM; 1/12° and 24 h resolution) experiments 60.5, 90.2, and 90.3, with currents at depths of 0, 10, 20, 30, 50, 75, and 100 m. We also used output from the Gulf of Mexico (GoM; 1/25° resolution and 24 h resolution) experiment 20.1, with currents at 0, 5, 10,

15, 20, 25, 30, 40, 50, 60, 70, 80, 90, and 100 m. The GoM model is run as a nested model with HyCOM; it uses the open boundary conditions from the HyCOM global analysis.

The virtual seascape was defined by the set of 261 coral reef habitat polygons used in a previous Caribbean-wide study of coral reef fishes (Cowen et al. 2006; Fig. S1). These polygons extend ca. 50 km along reefs, and include a 9 km buffer. This type of buffer is typically used in models of the resolution scale used here to account for a wide range of near-shore processes that cannot be fully resolved, including physical and behavioral phenomena. Larvae were released from the centroid of each habitat polygon and tracked until their maximum PLD. Simulated larva passing into a habitat polygon after their competency age were considered settled.

The CMS software enables the user to specify a vertical distribution that can change across simulation time to represent ontogenetic movements. Individual simulated larvae were moved between the specified depth layers, to force the overall population of larvae towards the specified age-specific distribution. Larvae can be moved by only one layer at each behavioral timestep, which is distinct from the hydrodynamic transport timestep (Appendix S1: Table S2). We utilized three vertical distributions: (1) surface-dwelling larvae, held at 1 m depth; (2) larvae that are uniformly distributed across 9 depth bins in the upper 100 m; and (3) a 9-depth generalized OVM behavior based on five taxa (two families: Pomacanthidae and Pomacentridae; one subfamily and one tribe: Anthiinae and Grammistini, both in the family Serranidae; one genus: *Xyrichtys* in the family Labridae; Fig. S2; more details in Appendix S1). For the OVM behavior, we set the simulation time (larval ages) for each distribution as 25% (distribution from size class 1), 25% (distribution from size class 2), and 50% (distribution from size class 3) of the pre-competency PLD. The last pre-competency distribution also applied through the competency period. In both the uniformly-distributed and OVM runs, at locations shallower than 100 m,

larvae were moved to an uniform distribution across 3 depths in the upper 25 m (again, they can be moved by only 1 depth bin at each behavioral timestep). Details of additional parameters are in Appendix S1: Table S2.

We selected two durations that correspond with peaks in the distribution of PLDs reported in a synthesis paper (Mora et al. 2012). Simulated larvae were competent to settle starting on day 20 in the “short” PLD simulations, representative of taxa such as the bicolor damselfish (*Stegastes partitus*; Sponaugle and Cowen 1996), as well as several other fishes in the families Labridae and Pomacentridae (Victor 1986a, Mora et al. 2012). For the “long” PLD simulations, simulated larvae were competent to settle starting on day 40, representative of taxa such as the bluehead wrasse (*Thalassoma bifasciatum*; Victor 1986, Sponaugle and Cowen 1997), as well as several other species in the families Labridae and Serranidae (Mora et al. 2012). In both cases, larvae remain competent to settle for a period of 10 days.

For each combination of behavior and PLD, 1000 larvae were released daily at midnight from January 2004 to December 2008 from approximately the centroid of each habitat polygon. *Analysis of simulation output*—The model output was processed using MATLAB 2019a. We calculated larval dispersal kernels using the total dispersal distance for all settled larvae from a given simulation (*i.e.*, a combination of behavior and PLD length). These distances were binned at 50 km intervals (*i.e.*, the approximate size of each polygon) from 0 to 3000 km, and the frequency of occurrence was normalized such that the kernel sums to one.

Connectivity matrices (Cowen et al. 2006, Botsford et al. 2009, Paris et al. 2013b) display the probability of larval transport from each source site (the rows, *i*) to the receiving sites (the columns, *j*). Each (*i,j*) entry is the proportion of releases from source polygon *i* that settle in receiving polygon *j*. Local retention is given by the diagonal entries of the connectivity

matrix—the probability of a propagule released from a given habitat patch settling in that same patch. Neither the connectivity matrix nor local retention are sensitive to the number of particles released or the egg production rate (Lett et al. 2015).

To address how behavior influenced connectivity, we defined a matrix, **C**, that measures the relative change in larval transport due to behavioral differences. Matrices **A** and **B** contain the counts of larvae transported from source node i to receiving node j under two behavioral scenarios. The entries of the matrix **C** are $c_{ij} = \frac{a_{ij} - b_{ij}}{\frac{1}{2}(a_{ij} + b_{ij})}$. This method scales the difference in the number of larvae transported from node i to node j (the numerator) by the average of the two matrix entries (the denominator). The c_{ij} are unitless and range between -2 to +2; $c_{ij} = \pm \frac{2}{3}$ indicates a doubling of larval transport from one behavior to the other, $c_{ij} = \pm 1$ indicates a tripling of larval transport between behaviors, and $c_{ij} = \pm 2$ indicates that the connection exists only under one of the behaviors. We choose to scale this way so that the comparison matrix **C** is symmetrical: if we swap the order of a_{ij} and b_{ij} , c_{ij} would change sign but not magnitude. This method cannot distinguish connections that change from 0 to 1 transported particle from those that change from 0 to 1000 transported particles (both would have a value of -2). A change from 0 to 1 particle being transported may be due more to stochasticity in the model as opposed to demonstrating a true new connection under one of the behaviors. To focus on connections, both behavior-dependent connections and those that are maintained between behaviors, that are less affected by stochastic transport events, we mask source-receiver pairs where the number of transported particles is 1000 or fewer in both **A** and **B**.

We used the MATLAB function **digraph** function to generate directed graphs from the connectivity matrices and the comparison matrices (**C**) and plotted these in geographic space.

For legibility, the connectivity maps are restricted to connections with at least 2% probability of larval transport. For the behavioral comparison maps, connections are shown if there was a 2% or greater probability of larval transport in at least one of the behaviors being compared *and* if the change in larval transport between behaviors was at least two-fold.

Results

Amongst the 14 families, two subfamilies, one tribe, and six genera investigated for ontogenetic patterns in larval vertical distribution, our analysis revealed a wide variety of behaviors (Fig. 1 and Appendix S1: Figs. S3 and S4). A persistent association with surface waters was seen in three families (Mullidae, Holocentridae, Fig. 1; Gerreidae, Appendix S1: Fig. S3; also see Appendix S1: Fig. S5). A downward ontogenetic vertical migration was evident in two families (Pomacentridae and Pomacanthidae, Fig. 1 and Appendix S1: Fig. S3; but note the small number of individuals in size class 3 for these two families), one subfamily (Anthiinae, Appendix S1: Fig. S4), one tribe (Grammistini, Fig. 1), and one genus (*Xyrichtys* sp., Fig. 1). In the other taxa, larvae showed a relatively consistent depth preference (e.g., Apogonidae, Fig. 1; Chaetodontidae, Appendix S1: Fig. S3), widened their preferred depth range with ontogeny (e.g., Acanthuridae, Fig. 1; Callionymidae, Appendix S1: Fig. S3), or exhibited non-systematic changes in depth preference (e.g., Gobiidae and Scorpaenidae, Fig. 1).

Dispersal kernels, representing the probability of larval settlement by distance from release site, showed higher probability of long-distance dispersal for surface-dwelling than for the other two behaviors (Fig. 2). The median dispersal distance of surface-dwelling larvae was greater than that for the uniformly-distributed and OVM larvae, by 39-47% for the short PLD simulations and by 29-39% for long PLD simulations. Surface-dwelling larvae also had a slightly

higher probability of settling: probability of success in the short PLD simulations was 43% for surface-dwelling larvae, while uniformly-distributed and OVM larvae experienced 38-39% successful settlement. In the long PLD simulations, settlement success for surface-dwelling larvae was reduced to 38% and 29-30% for uniformly-distributed and OVM larvae, but surface-dwelling larvae still showed considerably greater settlement success than deeper-dwelling larvae.

Our focal traits, vertical distribution behavior and PLD, have markedly stronger effects on dispersal than season or year. Dispersal kernels did not show strong seasonal variability in any of the 6 experiments (Appendix S1: Fig. S6). Median dispersal distance between seasons varied by 0-14%; the greatest difference was between the summer and fall quarters for surface-dwelling larvae with long PLDs (Appendix S1: Table S3). Likewise, dispersal kernels were very similar amongst the 5 years of simulations, with the greatest variability seen in the surface-dwelling larvae (Appendix S1: Fig. S7).

Overall, ontogenetically migrating and uniformly-distributed larvae experienced greater retention than surface-dwelling larvae (Fig. 3). Time spent in the plankton (PLD) decreased retention in most of the regions. However, the effect of surface-dwelling behavior on retention was strongest in the eastern Caribbean regions of Turks and Caicos, Venezuela, and the Windward and Leeward Islands, where habitat is spaced far apart and surface currents are influenced by directional circulation patterns. This contrasts with regions to the north and west where surface-dwelling and deeper-dwelling larvae experienced similar rates of retention, such as Nicaragua, Panama, Colombia, the Florida Keys, the Bahamas, and much of Cuba (Fig. 3).

Connectivity increased with a longer dispersal time, and changed with larval fish behavior (Appendix S1: Figs. S8, S9, S10). The deeper behaviors of OVM and

uniformly-distributed larvae constrained connectivity relative to surface-dwelling behavior, which resulted in greater connectivity among reef sites. The connectivity maps, which focus on strong links with a transport probability of $\geq 2\%$ (Appendix S1: Figs. S9, S10), show more regional structure in the connectivity network for deeper behaviors compared to surface-dwelling larvae.

The effect of behavior on connectivity can be visualized more clearly from the relative difference in the transport of larvae amongst reef sites between behaviors (Fig. 4 and Appendix S1: Figs. S11, S12, S13). These plots confirm that there is an overall pattern of greater dispersal in surface-dwelling than in OVM simulations (Fig. 4A, redder at off-diagonal sites; Fig. 4C, long red links) and greater local retention in OVM simulations (Fig. 4A, blue is seen mostly along the diagonal; Fig. 4C, short blue links and blue self-loops). Behavior-dependent connections, wherein a given source-receiving node pair had larval transport under one behavior and not the other, were more likely to occur with surface-dwelling behavior than OVM behavior. There were 538 connections that appear for surface-dwelling larvae but not for OVM larvae with short PLD and 703 with long PLD, and there were 21 behavior-dependent connections for OVM but not for surface-dwelling larvae with short PLD and 26 with long PLD.

The comparison matrices and maps also underscore the similarity in dispersal and connectivity patterns for the two deeper behaviors (Fig. 4B,D and Appendix S1: Fig. S13). The plot of change in larval connectivity between the surface-dwelling and uniformly-distributed simulations (Appendix S1: Fig. S12) shows similar patterns as observed for the comparison between surface-dwelling and OVM larvae (Fig. 4A,C and Appendix S1: Fig. S13). Uniformly-distributed behavior led to slightly greater transport than OVM (Figs. 4B,D and Appendix S1: Fig. S13), but the changes were much smaller than observed between the

surface-dwelling behavior and either of the deeper behaviors (Figs. 4 and Appendix S1: Figs. S11, S12, S13). Likewise, the comparison map of uniformly-distributed and OVM simulations (Fig. 4D) shows that very few strong links exhibited a large change between the two subsurface behaviors.

Discussion

In this study, we comprehensively examined vertical distribution patterns across the larval period for multiple taxa of coral reef fishes, finding distinct and notable differences both within and among coral reef fish families. We found that OVM behaviors were common, appearing in five taxa, but we also observed other prevalent sub-surface behaviors. As such, we used simulations to investigate how two deeper behaviors—OVM and uniformly-distributed larvae—compare with surface-dwelling larvae in terms of potential dispersal and connectivity.

We found that surface-dwelling fish larvae—representative of, for example, the often-abundant goatfishes and mojarras—disperse substantially longer distances than either of the deeper behaviors. Furthermore, the dispersal and connectivity of the two deeper behaviors were surprisingly similar. In other words, a uniform vertical distribution had essentially the same benefits for increased local retention as the more complex OVM behavior. This suggests that an age-specific pattern of increasing depth is not required to restrict dispersal in the pelagic zone.

In contrast to these overall results, retention and connectivity on a regional and local basis showed spatial variation in which traits maximize dispersal or connectivity.

Surface-dwelling larvae were as likely as deeper-dwelling larvae to be retained in Panama, Nicaragua, and Florida (Fig. 3), while OVM and uniformly-distributed larvae were more likely than surface-dwelling larvae to be exchanged from Panama to Colombia (Figs. 3, 4, and

Appendix S1: Figs. S11 and S12). Surface-dwelling larvae are entrained by wind-driven circulation, which carries them predominantly to the northwest in the Caribbean (Tang et al. 2006). Other studies have found that a cyclonic gyre in the Gulf of Honduras drives retention and connectivity in the Mesoamerican reefs (Tang et al. 2006, Butler et al. 2011, Martínez et al. 2019). Because of the complex interactions among larval behavior, PLD, ocean currents, and habitat availability, the same larval vertical behavior can lead to different dispersal and connectivity outcomes, and concomitant population effects, across regions. Therefore, pan-Caribbean species might have regional differences in behavior or PLD (e.g., especially in species that exhibit an extended competency period like the bluehead wrasse (Victor 1986b, Sponaugle and Cowen 1997)), or distinct population genetic structure across regions (Kool et al. 2010, Selkoe et al. 2014, Truelove et al. 2017).

The diversity of larval vertical behaviors that we observed, and their strong effect on dispersal and population connectivity in our simulations, indicate that these behaviors can play a role in coral reef fish population persistence and evolution (Sponaugle et al. 2002, Strathmann et al. 2002). Furthermore, our results shed light on how larval traits could have evolved to maximize the chance of reaching suitable settlement habitat, particularly if we consider that suitable habitat may be distributed in accordance with other traits of each species. For example, if intraspecific competition for resources is low for adult and juvenile fish of a given species, then retention near suitable habitat—i.e. where the adults spawned—may be a successful strategy (Waser 1985, Hovestadt et al. 2001, Burgess et al. 2014). In this case, traits such as deeper-dwelling larvae can restrict dispersal and also facilitate local adaptation (Strathmann et al. 2002). Alternatively, if intraspecific competition is high and spawning adults are already near carrying capacity, then suitable habitat would be elsewhere and longer-distance dispersal would

increase the probability of settlement and recruitment. Therefore, we might expect species with surface-dwelling larvae to show less local adaptation.

Habitat specialization could also be evolutionarily linked with larval behaviors for modulating dispersal distance. Habitat generalists may be less constrained by settlement site suitability, which could allow for the evolution of surface-dwelling larvae and long-distance dispersal. For example, Mullidae larvae do not require a specific settlement site at the end of their larval duration, since they remain in pelagic feeding aggregations into the juvenile period before shifting to demersal habitat such as seagrass and sandy reef areas (Munro 1976). On the other hand, several of the taxa that we identified as deeper-dwelling have stricter settlement habitat requirements: serranid larvae require habitat structure such as rocky reefs for settlement (Thompson and Munro 1984), and pomacentrid larvae preferentially settle on live coral (Booth and Beretta 1994).

In considering the evolution of larval fish traits, it is important to evaluate trade-offs. While simulated surface-dwelling larvae dispersed farther and had a higher overall probability of settling compared to deeper-dwelling larvae, life in the surface waters comes with greater risks of starvation, predation, and UV damage. Distributions of chlorophyll and zooplankton generally show a peak in the subsurface, with lower values at the very surface (Hopkins 1982, Llopiz 2008, Espinosa-Fuentes et al. 2009). Surface-dwelling larvae are typically heavily pigmented to protect against UV damage, but the high light and the dark pigmentation both increase visibility of larvae to their predators. To deter predators, surface-dwelling larvae in the family Holocentridae develop long spines. For species that adapt to a larval period in the surface waters, the lower competition, higher temperatures, and greater dispersal must outweigh the dangers of increased mortality and the energetic costs of physical protections (e.g. spines and pigmentation).

If other sub-surface behaviors can replicate the dispersal and connectivity of OVM, then what other selective pressures may lead to the prevalence of OVM in coral reef fish taxa? A major advantage associated with OVM is related to growth and predation risk: by being in warmer surface waters at the beginning of larval life, individuals can grow out of the most vulnerable phase quickly. Previous work suggests yolk-sac larvae concentrate in the upper water column both because of predator avoidance (non-visual large zooplankton) and limits on their ability to feed at low light, while older larvae tune their vertical distribution to food availability (Fortier and Harris 1989, Job and Bellwood 2000). Deeper waters may also increase the ability of a competent larva to reach settlement habitat, both because they may be able to overcome the slower horizontal currents at depth by swimming and because the colder temperatures at depth may contribute to an extension of the competency period (Green and Fisher 2004).

In addition to the traits that we examine in this study, there are myriad processes that determine the successful settlement of larval coral reef fish. Larval growth rates, and therefore often the PLD, depend on temperature and food availability (Houde 1989). Larval mortality rates generally decrease with size (Houde 1997) and will vary spatially—horizontally due to patchy predator distributions and vertically due to predator behaviors and light availability. While mortality rates can have important impacts on modeled population connectivity and recruitment (Cowen et al. 2006, Paris et al. 2007), true recruitment and demographic connectivity will also depend on tradeoffs among larval traits (*e.g.*, behavior, growth rate, PLD, mortality) as well as adult traits (*e.g.*, longevity, fecundity, spawning periodicity; Cowen et al. 2006). Horizontal swimming ability increases with size and fin development (Peck et al. 2012), and larvae may use directional swimming in response to cues as they prepare to settle (Leis 2006, Paris et al. 2013a). Nearshore physical processes, including tides, internal waves, and coastal boundary currents can

also affect larval transport and settlement (Pineda et al. 2007). As models increase in complexity, more of these processes can be incorporated.

It can be difficult to compare simulation results with empirical measures of dispersal and connectivity because the studies, and the mechanisms that they can detect, operate on different spatial and temporal scales (Skogen et al. 2021). Estimates of genetic connectivity based on microsatellite loci are often on the order of 500-1000 km (Purcell et al. 2006, 2009)—getting into the tails of the dispersal kernels that we simulated—but these studies estimate connectivity that occurs over multiple generations. In a study of bicolor damselfish on Mesoamerican reefs, otolith microchemistry shed light on dispersal at the between-atoll scale (100-200 km separation), indicating that the majority of settlement occurred within that distance (Chittaro and Hogan 2013). This is consistent with our dispersal kernel from the simulations that most closely resemble *S. partitus*: OVM behavior and short PLD. Genetic methods for single-generation dispersal have estimated shorter distances than we resolve in our simulations: 6-50 km along the Mesoamerican Barrier Reef for five species of coral reef fish (Puebla et al. 2012), and 10 km for yellowhead jawfish (a mouth brooder with PLD of 15-21 days) in Puerto Rico (Beltrán et al. 2017). The five species studied in the Mesoamerican Barrier Reef (Puebla et al. 2012) include one for which OVM has been documented (*Stegastes partitus*; Paris and Cowen 2004), three from groups that we showed here do not undergo OVM (*Thalassoma* spp., Chaetodontidae, and Serraninae), and one which exhibits a demersal, inshore behavior as larvae (Haemulidae; Lindeman et al. 2001). This mismatch in single-generation estimates of dispersal between biophysical models and genetic measures suggests that the models are missing important processes, which could include spatially-variable larval mortality, additional larval behaviors and responses to sensory cues, or post-settlement mortality that selects for recruits that originated

nearby. Valuable recent studies combine biophysical models and genetic data to investigate dispersal and identify important realistic larval traits (Bernard et al. 2019, Bode et al. 2019), and future work should focus on the synthesis of models and observations.

The experiences of planktonic larvae, from their large-scale transport in ocean currents to their small-scale movement in response to both biotic and abiotic cues, remain difficult to study. Although biophysical modeling is one of our strongest tools for forming and testing hypotheses about larval dispersal and connectivity, there is a lack of detailed knowledge of the behaviors of many species. Empirical studies should continue to focus on describing both observed patterns of larval behavior, such as the vertical distributions that we present here, as well as mechanistic studies of how larvae behave on small scales and what settlement cues they respond to—e.g., olfaction (Gerlach et al. 2007) and sound (Montgomery et al. 2006). On the modeling side, important progress has been made over the last couple of decades to model exchange between nearshore shallow environments and the open ocean, but more improvement is still needed (Swearer et al. 2019, Fringer et al. 2019). Our results focus on the transport of larvae in the open ocean at broad spatial scales, and demonstrate increased local retention and regional structuring for larvae following empirically-derived sub-surface behaviors. These results can inform hypotheses for future studies of larval behaviors, local adaptation, and population structure. These results can also guide reef management by providing some intuition about how climate change impacts on oceanographic patterns, stratification and larval development time might alter connectivity. By focusing on vertical distributions as functional traits, we reduce the dimensionality of the question of connectivity for a given fish community.

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Figure Legends:

Figure 1. Selected ontogenetic vertical distributions. Each row of panels represents a different taxon. The first 7 rows are Family-level taxa, and the final 2 rows are at a lower taxonomic level: Grammistini is a tribe in the Family Serranidae, and *Xyrichtys* is a genus of the Family Labridae. The columns of sub-panels refer to size classes (SC) 1 through 3 that represent respectively 25, 25, and 50% of the observed size range. Each sub-panel shows the proportional abundance in 4 depth bins in the upper 100m, and the total sample size (n) for each taxon and size class. Each row is labeled with the taxon name and the size range. An asterisk at the upper end of the size range indicates that there were outliers for that taxon (See Appendix S1: Table S1).

Figure 2. Overall dispersal patterns. Dispersal kernels of successfully settled larvae for combinations of larval behavior and pelagic larval duration (PLD). The kernels are plotted as probability densities in 50-km wide bins and frequencies are normalized such that the sum of all bars is equal to 1. The median dispersal distance is numerically displayed and shown as a vertical dashed line. Note that all 6 sub-panels have the same horizontal and vertical axes. (Rows) Three larval behavior simulations were conducted: surface-dwelling, uniformly-distributed, and ontogenetic vertical migration (OVM). (Columns) Short and long PLD simulations correspond to 20-30 days and 40-50 days, respectively.

Figure 3. Mean local retention in each region, by behavior and pelagic larval duration (PLD). The height of each bar is the mean value of retention for all habitat polygons in each region, where retention is the proportion of successful larvae that settled in the same habitat polygon as their release site. Error bars show the standard error of the mean. Regions are arranged roughly west to east (**A** and **B**). Below, a map of the regions is provided as a key (**C**). Habitat polygons are colored to differentiate regions, but colors have no meaning.

Fig. 4. Relative change in larval transport between the surface-dwelling and OVM simulations, and between the uniformly-distributed and OVM simulations, for long PLD. Entries in the relative change matrices (**A** and **B**) are given by $c_{ij} = \frac{a_{ij} - b_{ij}}{\frac{1}{2}(a_{ij} + b_{ij})}$, where the a_{ij} is the larval transport for surface-dwelling larvae (**A**) or uniformly-distributed larvae (**B**) and b_{ij} is the larval transport for OVM larvae (**A** and **B**). Rows within each matrix correspond to release sites (source nodes) and columns to settlement sites (receiving nodes). Red colors indicate more larvae transported in the surface-dwelling (**A**) or uniformly-distributed (**B**) simulations. Blue colors indicate more larvae transported in the OVM simulations (**A** and **B**). Source and receiving nodes

are grouped within regions, arranged roughly west to east (see Fig. 3C for a map with regions labeled). The maps (**C** and **D**) display important links between habitat patches that change by at least a factor of two between behaviors (absolute value of relative change metric greater than or equal to 2/3). Important links are defined as those with at least 2% connectivity probability in one of the behaviors being compared. Self-loops are included.







